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23. Hewlett-Packard model 6824A.
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26. We thank L. J. Peterson of the University of California at Davis for the scanning electron micrograph, G. W. Krantz for the micrograph, and M. A. Strand and R. G. Peterson for statistical analysis. Supported by the Oregon State University Research Foundation. This is *Oreg. State Univ. Agr. Exp. Sta. Tech. Pap. No. 3120.*

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Altruistic Behavior in a Sphecid Wasp: Support for Kin-Selection Theory

Abstract. Trigonopsis cameronii *females often work in groups of up to four individuals on single nests, and because of inbreeding and a tendency to return to the mother nest, nestmates are likely to be highly related. The altruistic behavior associated with group living, most notably the failure to steal prey from nestmates, can thus be explained by kin-selection theory.*

Sociality has evolved independently at least 11 times in the order Hymenoptera (*1*, *2*), but the only known social species in the family Sphecidae is in the genus *Microstigmus* (Pemphredoninae) (*2*). In this report the behavior of a second, apparently independently social sphecid, *Trigonopsis cameronii* Kohl (Sphecinae) (*3*), is described, and it is shown that, as predicted by Hamilton's kin-selection theory (*4*), altruistic behavior associated with sociality is maintained in this species within groups of highly related individuals.

A *T. cameronii* female spends from about ½ to 1½ days building or renovating a cylindrical mud cell (renovation was always shorter than construction). She then captures and paralyzes a cockroach and carries it to her nest, lays an egg on it, places it in the cell, and closes the cell with a mud cap. After spending 1 to 3 relatively inactive days on the nest, she opens the cell, and over the next 1 to 7 days she adds more paralyzed roaches. Foraging for roaches occurs only from about 8 a.m. to 3 p.m. (the "work day"), and the wasp closes the cell at the end of each day's foraging, to open it at the beginning of the next work day. When the cell is sufficiently full (the number of roaches varied with their size, and was usually between 7 and 14), the female closes it and begins another. The egg in the cell hatches about 2 days after it is laid, and the larva consumes the roaches provided by its mother, pupates, and emerges as an adult about 50 days after the original oviposition. Males rest on groups of cells during the work day and mate with females as they emerge.

Nests occurred in sheltered, at least somewhat humid sites, such as under overhanging boulders at the edges of streams, and contained up to 130 cells. From one to four females were found working on cells in a given nest. The females almost always concentrated their building and foraging efforts on their own cells, but in certain situations they performed relatively minor behavior benefiting nestmates. They actively repelled ants on or near the nest (males also chased ants from nests). Females which had constructed new cells often added mud to the sides and back of the nest during the work days between oviposition and provisioning, and although most of this material was added to the wasp's own cell, some was added to others. Holes in cells containing pupae, occasionally caused by a female taking dirt from such a cell to close or renovate her own, were closed, sometimes by the female which caused the damage and sometimes by others.

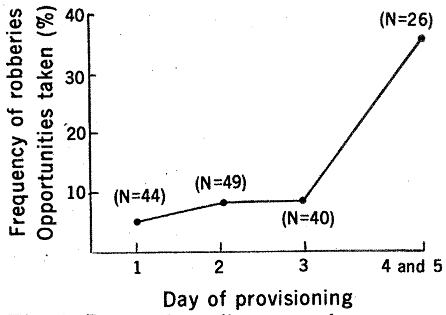

Fig. 1. Rates of stealing at various stages of provisioning (*N* is the number of observations).

The most striking altruistic behavior of *T. cameronii* involved the stealing of roaches captured by nestmates. Every time a female provisioning a cell arrived at the nest while a nestmate's cell was open and partially filled with roaches, she had the opportunity to steal them and put them in her own cell. Although apparently all females were capable of robbing (10 of 11 individuals observed for extended periods committed robberies), stealing was the exception rather than the rule (Fig. 1). Also, in no case did a female steal all the roaches available in a nestmate's cell, and usually (16 of 18 cases) she stole only one. In addition, cell owners very seldom made any attempt to prevent robberies. Although females often entered nestmates' open cells, I witnessed only one aggressive interaction apparently occasioned by one female attempting to enter another's cell, and I saw three robberies committed while the second female was present but she offered no resistance.

There are indications that robberies tend to occur in times of "need," that is, poor hunting success. They were more common during the last days of provisioning, especially when the wasp was unable to finish within 3 days [(*5*); Fig. 1]. All the robberies that did occur in the first 2 days of provisioning (five observations) happened in the last half of the work day and, in four cases, after especially unsuccessful hunting activity. The single aggressive interaction involving entry into a cell occurred between two females, each of which had had poor hunting success and had already robbed from the other; one was in her fourth day of provisioning and the other in her third.

The tendency to rob probably did not involve danger of the larva starving. Eggs hatched about 2 days after being laid (usually about the time provisioning started), and the new larva spent about the next 2 days feeding on the roach on which the egg was laid. One larva in captivity fed continuously but had eaten only four roaches (*6*) 4 days after its mother opened its cell to begin provisioning (that is, at the beginning of what would have been the fifth day of provisioning, approximately 6½ days after the original oviposition). Thus, larvae were probably usually just starting to feed on provisioned roaches during the last days of provisioning when the females tended to rob.

Robbery of a cell, which involved one wasp discarding the contents of another wasp's cell and laying her own egg there, was seen only once, although the opportunity (one wasp ready to start a new cell, another with an open cell on the same nest) occurred 14 times. The female which committed this robbery had taken unusually long (7 or 8 days) to finish provisioning her previous cell.

By marking wasps as they first emerged from their cells, it was possible to show that the wasps on a given nest are probably often highly related. Five (perhaps six; one mark was equivocal) of eight females marked with model-airplane dope as they emerged returned to within 0.5 m of their mother nest 3 days after they emerged, and three (perhaps four) of them subsequently provisioned cells there. One of two males marked as they emerged also returned to his mother nest and subsequently mated with females emerging there (the other male was only poorly marked and may have returned but without his mark). Individual males patrolled the same nest each day for up to more than a month and chased other males from the site.

Thus, it is likely not only that a given wasp's nestmate is her sister, but also that the nestmate mated with the given one's brother. This mating system implies especially high relatedness with the offspring of nestmates. In other words, the altruistic behavior just described is performed to benefit individuals that are probably usually highly related, as predicted by Hamilton.

The pattern of robberies also conforms to Hamilton's predictions: robberies may usually occur only in situations of need because otherwise possible damage to the probably highly related offspring of nestmates would outweigh the benefits of a given wasp's offspring; and the fact that robberies are so restricted suggests that the cost to a wasp of permitting a robbery could be outweighed by the benefit to its own genes present in its neighbor's offspring.

The level of sociality exhibited by *T. cameronii* is very low, with no signs of the division of labor associated with many insect societies (*7*). Probably as a result of highly viscous populations, however, these wasps have developed behavior which overcomes the tendency toward intraspecific parasitism which is associated with the first steps of evolution from solitary to group life, and they derive the benefits (periodic nest defense, ready-made cells, and at least occasional reserves of prey in times of need) that group living provides.

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References and Notes

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2. R. W. Matthews, *Science* **160**, 787 (1968); *Psyche* **75**, 1, 23 (1968).
3. The general biology of *T. cameronii*, with more detailed descriptions of most of the characteristics mentioned here, is in preparation. This study was conducted near Cali, Colombia (4°N latitude); the species occurs in Central America and northern South America.
4. W. D. Hamilton, *J. Theor. Biol.* **7**, 1, 17 (1964).
5. The average number of days spent provisioning, measured to the nearest half day, was 3.3 days (31 observations), range 1.5 to 5.0, median and mode 4.
6. The number of roaches consumed depended on their sizes. This larva ate one small and three medium-sized roaches.
7. By some criteria, such as those of C. D. Michener [*Annu. Rev. Entomol.* **14**, 299 (1969)] or E. O. Wilson [*The Insect Societies* (Harvard Univ. Press, Cambridge, 1971)], this species should be considered communal rather than truly social.
8. Supported by a grant from the Comité de Investigaciones, Universidad del Valle. I thank Dr. H. E. Evans for identifying the wasps and Dr. M. J. W. Eberhard and C. Garcia for stimulating discussions.

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Evolution of DNA Base Compositions in Microorganisms

Singer and Ames (*1*) proposed that ultraviolet light exerts a selective pressure for high percentages of guanine (G) plus cytosine (C) in the DNA (G + C content) of bacteria exposed to sunlight. They gave several examples of bacteria having both high G + C contents and what they considered to be a large amount of exposure to sunlight (organisms that form aerial conidia or fruiting bodies produce carotenoids to protect against photooxidation, or have a habitat near the surface of water). They also suggested as the most likely explanation for low G + C contents in bacteria some weaker selective pressures that are overwhelmed when the organism occupies a niche with high ultraviolet exposure. As possible weaker selective pressures they mentioned ionizing radiation and the natural occurrence of some alkylating chemicals. In support of this idea they gave several examples of obligate anaerobes and internal parasites all of which have low G + C contents. They noted only two examples (*Cytophaga* and *Saprospira*) that were difficult to explain by their theory.

Other bacteria may also be exceptions (Table 1). Bacteria which are well-adapted parasites of man and animals, according to the theory, are expected to have low G + C contents. The parasitic bacteria listed in Table 1 grow best at 37°C; in addition most of these bacteria are fastidious, and many are strict anaerobes. Generally, they cannot survive for very long outside their hosts, and the number of these bacteria which are exposed to sunlight must be very small. Some bacteria from aquatic environments also seem to be exceptions. One could not expect to find bacteria with a high G + C content in deep sea sediments. Some strictly anaerobic and nonphotosynthetic bacteria (*Desulfovibrio* and some *Spirochaeta*) are presumably not exposed to ultraviolet and these also have high G + C contents. In contrast, many pigmented and strictly aerobic bacteria, which are generally found near the surface of the water, have low G + C contents. It seems that most true marine bacteria, except for some micrococci, characteristically have lower G + C contents than their terrestrial counterparts. This is noteworthy, as a high proportion of marine bacteria occur in the zone of water exposed to sunlight ultraviolet.

An evaluation of the degree to which terrestrial bacteria are exposed seems more difficult. Singer and Ames judged members of the genus *Rhizobium*, 63 percent (G + C content is given as a percentage after the genus), to have a high exposure to sunlight. These organisms are adapted to grow on the roots of legumes where they form nodules. These and many other bacteria